

Silk Glands in Adult Sphecid Wasps (Hymenoptera, Sphecidae, Pemphredoninae)

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Abstract.—Among the sphecid wasps, females of the genus *Psenulus* and some members of the subtribe Spilomenina are known to use silk for nest lining. In *Psenulus*, this behavior has been reported for a long time, but the source of the secretion has never been correctly recognized. Most authors have considered the lining material as derived from salivary glands. Dissection and KOH clearing of dried specimens and dissection of fixed specimens revealed that the glands in *Psenulus* are associated with the 4th and 5th sterna of the females and in the subtribe Spilomenina, they are associated with the 6th tergum. In both groups, the glands are composed of class 3 epidermal cells, in the classification of Noirot & Quennedey (1974). In *Psenulus*, the secretory cells associated with each sternum are numerous, exceeding one hundred. The duct cells are very long and their opening on the integument is usually surrounded by cuticular seta-like projections, here called setiform spinnerets. In most cases, each spinneret includes more than one duct. External examination of 33 species of *Psenulus* revealed that the size, number and distribution of the setiform spinnerets are quite variable; moreover, the spinnerets are absent in the Neotropical group of species. In the subtribe Spilomenina, the secretory cells have the same morphology, but the setiform spinnerets are located at the apex of the 6th tergum. Several authors have misinterpreted this area in *Spilomena* as a pygidial plate. The shape, arrangement and location of the spinnerets vary greatly among species of *Spilomena*. Despite the similarity in morphology, the silk glands in *Psenulus* and Spilomenina probably evolved independently.

INTRODUCTION

Production of silk or silk-like materials by adult insects is relatively rare and restricted to a few groups (Rudall and Kenchington 1971, Kenchington 1984, Sehnal and Akai 1990). Among Hymenoptera, it has been reported for *Eupelmus* (Chalcidoidea, Eupelmidae; Delanoue and Arambourg 1965), *Signiphora coquilletti* Ashmead (Chalcidoidea, Signiphoridae; Woolley and Vet 1981), *Quartinia vagepunctata* Schulthess (Vespidae, Masarinae; Gess and Gess 1992), *Polistes* (Vespidae; Singer *et al.* 1992), *Hylaeus* (Apoidea, Colletidae; Espelie *et al.* 1992) and for two groups of sphecid wasps (Apoidea).

These two groups of sphecid wasps belong to the subfamily Pemphredoninae: the genus *Psenulus* (Psenini) and two genera of the subtribe Spilomenina, *Microstigmus* and *Arpactophilus* (Pemphredonini).

In these wasps, silk is secreted only by females and is used in nest construction. Myers (1934) was the first to suggest that the nests of *Microstigmus theridii* Ducke were built with plant hairs held together by some kind of silk. Matthews (1968), based on observations of females of *M. comes* Krombein rubbing the tips of their abdomens over the nests and on dissections (KOH clearing of metasoma), suggested that the glands associated with the setal brush at the tip of tergum VI were involved in the production of silk. Matthews and Naumann (1988) found that *Arpactophilus mimi* Naumann builds its nest inside abandoned mud cells of *Sceliphron* wasps using only silk. The authors say that the silk is secreted from glands near the tip of the metasoma, and that these

glands appear to be homologous with those of *Microstigmus comes*. Carvalho and Zucchi (1989) mention briefly the use of silk for cell lining in *Spilomena*, but do not comment on the source of the silk.

Since the early studies of the nesting biology of *Psenulus*, it has been recognized that females use some sort of silk to line the nest walls and to make partitions between brood cells (Maneval 1932, Grandi 1934, 1935, Iwata 1938, Leclercq 1941). However, the source of the silk was never correctly recognized. Grandi (1935) was the first to suggest that the silk was secreted by the females, although he presented no evidence for the nature of the putative glands. Janvier (1975), based on evidence of use of salivary secretions in nest lining by colletid bees and on his own dissections of the mouthparts of *Psenulus concolor* (Dahlbom), concluded that the silk produced by *Psenulus* was secreted by labial glands. The labial structures illustrated by him seem to be some type of sensilla or may be openings of a true labial gland, but certainly these glands would not be responsible for the large amounts of silk found in the nests. Small epidermal glands are widespread in the mouthparts of social vespids (Landoldt and Akre 1979). Florin and Bricteux-Grégoire (1961) demonstrated that the substance secreted by females of *P. concolor* is silk. They found an amino acid composition similar to that of silk produced by other insects and spiders. In this paper, I describe for the first time the silk glands of *Psenulus*. Additional information on the morphology and taxonomic distribution of silk glands within Spilomenina is also presented.

MATERIAL AND METHODS

Most of the material used in this study were pinned museum specimens that were examined only under a dissecting microscope (up to 126 \times). A few dried, pinned specimens of *Psenulus frontalis* (Fox), *P. mayorum* Bohart & Grissell, *P.*

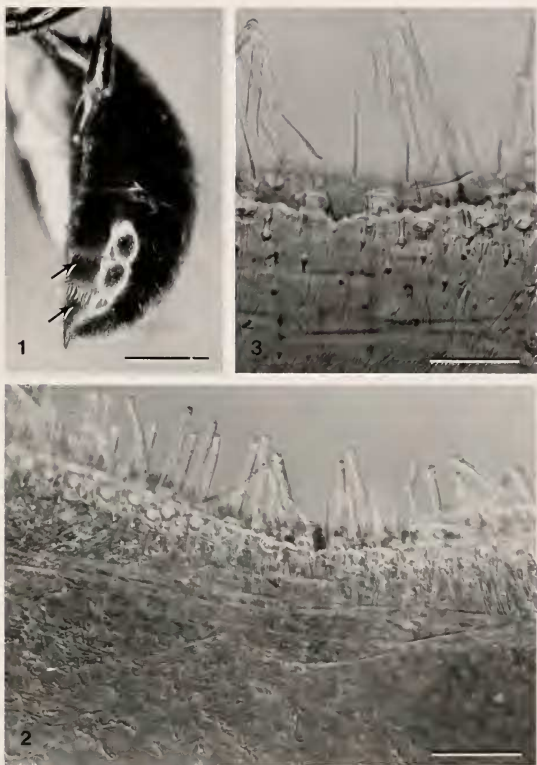
puncticeps (Cameron), and *Spilomena* sp. (from Australia) were dissected and had their sterna or terga cleared with KOH. Also, a few fresh and fixed (Kahle's fluid) specimens of *Psenulus mayorum*, *Microstigmus nigrophthalmus* Melo, *Spilomena alini* Antropov, *S. pusilla* (Say), *Spilomena* sp. (from Brazil) and *Xysma* sp. (from Brazil) were dissected. The dissected material was examined and photographed with an Olympus BH-2 microscope with differential interference contrast optics. The pinned specimens were photographed under an Olympus SZH dissecting microscope. In the descriptions, the term metasoma (Michener 1944) refers to the abdomen excluding the first segment (the propodeum). The metasomal sclerites are numbered with Roman numerals.

RESULTS AND DISCUSSION

Psenulus

Upon external examination, females of *P. frontalis* were found to have a row of long pale bristles on the apex of sterna IV and V (Fig. 1). These bristles have a blunt tip and are much thicker than the regular setae found on the sterna (Fig. 2). Their length varied from 120 to 155 μm , and an average of 47 bristles (range 41 to 56) was found on sternum IV and 51 (46 to 57) on sternum V. The bristles on sternum V are somewhat differentiated into two rows, the anterior row with shorter bristles. Examination of cleared specimens showed that these bristles were associated with long ducts of class 3 epidermal glands [in the classification of Noirot and Quennedy (1974, 1991)]; see Fig. 2. Numerous individual ducts enter each bristle and open at the bristle tip (Fig. 3).

Class 3 epidermal glands are widespread among insects (Noirot and Quennedy 1974), and a great number of glands in Hymenoptera are known to be composed with this kind of secretory unit (e.g. Youssef 1975, Hölldobler and Engel 1978, Landolt and Akre 1979, Jeanne *et al.* 1983,



Figs. 1-3. Metasoma of *Psenulus frontalis*. 1. Lateral view, showing the setiform spinnerets (arrows); scale = 0.8 mm. 2. Posterior margin of a cleared sternum IV, showing the spinnerets and ducts of the silk glands; scale = 0.1 mm. 3. Enlargement of part of Fig. 2, showing spinnerets with several cell ducts entering it; scale = 50 μ m.

Billen 1987, Cruz-Landim 1987). In most cases, the ducts open individually on the surface of the integument and are not associated with any special cuticular pro-

tuberance. Ducts opening at tips of bristles, as in silk glands of *P. frontalis*, have been reported for abdominal glands in males of *Campodea* (Diplura) and silk

glands of machilids and lepmatids [see review in Bitsch and Bitsch (1991)], for an antennal gland in males of *Trissolcus* (Hymenoptera; Bin and Vinson 1986), for tarsal silk glands in males of empidids (Diptera; Eltringham 1928) and for tarsal silk glands of embiopterans (Nagashima *et al.* 1991).

With the possible exceptions of *Campodea* and *Trissolcus*, these glands are involved in the production of silk, and the bristles seem to be acting like spinnerets in the formation of silk threads. Bitsch (1990) named these special bristles as tubular bristles, while Bitsch and Bitsch (1991) called them glandular bristles. Considering the similarities in development among the different epidermal organules [sensillae, class 3 glandular cells, non-innervated setae, scales; reviewed in Gnatzy and Romer (1984)], it seems reasonable to consider these tubular bristles homologous only to the external part of setae and sensillae. In this case, the name glandular bristle seems preferable, since it makes reference to the whole organule, and not only to the external protuberance, as tubular bristle does. For the glands associated with the production of silk, I will refer to these cuticular protuberances as setiform spinnerets or just spinnerets (Fig. 4A).

In all the 33 additional species of *Psenulus* examined, the females have some sort of setiform spinnerets on the apices of sterna IV and V, with the exception of 3 species (*P. aztecus*, *P. mayorum*, and an undescribed species from Mexico), all belonging to the group occurring in the Neotropical region (5 species known to me). Among the species with spinnerets, 11 of them have long spinnerets distributed in a narrow band on the sternal apex, as in *P. frontalis* (*P. aurifasciatus*, *P. calae*, *P. erusus*, *P. freetownensis*, *P. laevigatus*, *P. pallipes*, *P. patei*, *P. paulisae*, *P. tanakai*, *P. trisulcus*, *P. turneri*), while the remaining species have shorter and more numerous spinnerets distributed in broader bands on

the sternal apex (*P. alienus*, *P. bakeri*, *P. bidentatus*, *P. capensis*, *P. carinifrons*, *P. interstitialis*, *P. latiannulatus*, *P. leoninus*, *P. lubricus*, *P. luteopictus*, *P. luzonensis*, *P. nigeriae*, *P. onewi*, *P. philippinensis*, *P. puncticeps*, *P. scutatus*, *P. xanthognathus*, an unidentified species from Taiwan, and an undescribed species from Sierra Leone). In several species of the latter group, the width of the bands differed between sterna IV and V, with the band on sternum V always broader than the one on sternum IV.

In *P. puncticeps*, the bands do not differ in their width. The spinnerets are very numerous (over one hundred in each sternum) and approximately 40 μm long. Apparently, one to four ducts are associated with each spinneret (the spinnerets disappeared with the KOH clearing).

The condition in the Neotropical species is very peculiar. Sterna IV and V each have a broad semi-circular area covered with long erect setae (40 to 85 μm long in *P. mayorum*; longer setae toward sternum apex), located medially in the segment. Examination of the cleared sterna of *P. mayorum* showed that the ducts open directly on the integument surface (apparently individually, and not in groups) and do not have associated spinnerets. The silk is probably applied with the help of the erect setae. The absence of spinnerets and the more disperse distribution of the duct openings on the sterna suggest that this might be the primitive condition for the genus, while the opening of the ducts restricted to a band on the apex of the segment and associated with spinnerets evolved later. However, the phylogenetic relationships among the species in this genus have not been analyzed and the proposed transformation series can not be evaluated.

Subtribe Spilomenina

The silk glands of this group are also composed of class 3 epidermal cells (Fig. 5). However, the setiform spinnerets and associated silk glands are located in the

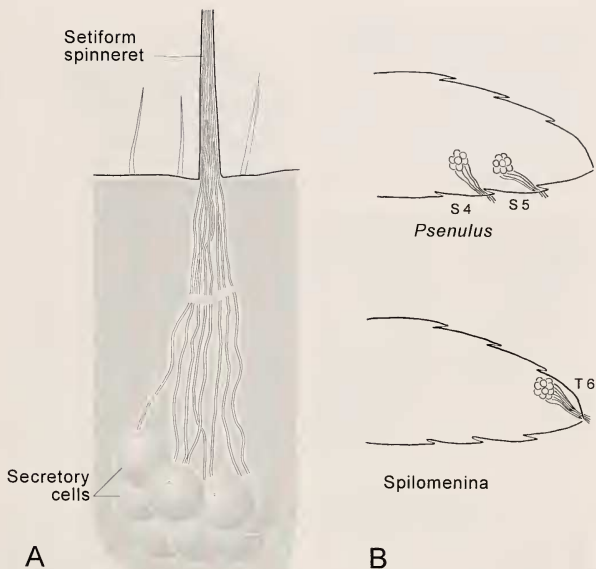
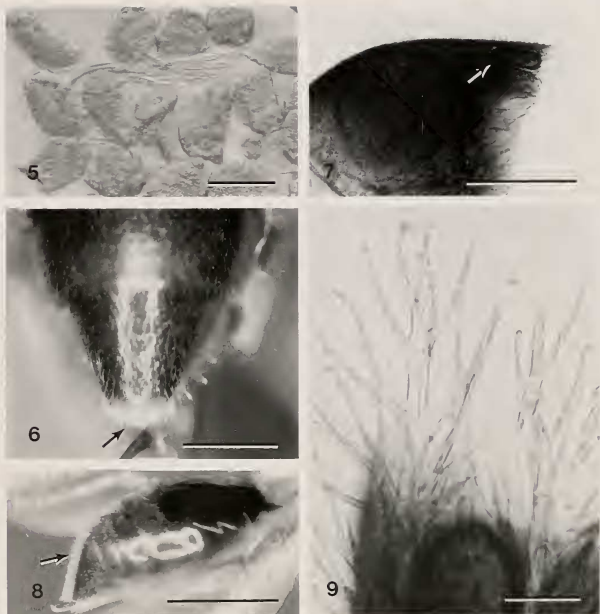


Fig. 4. A. Diagram of a group of glandular cells and ducts associated with a spinneret. B. Diagram showing the position of the silk glands in the metasoma of females in the genus *Psenulus* and in the subtribe *Spilomenina*.

tergum VI (Fig. 6). Three main lineages can be recognized in this subtribe (Melo, in prep.): *Arpactophilus*, *Spilomena* + *Microstigmus* + *Xysma*, and *Spilomena subterranea* McCorquodale & Naumann plus related undescribed species.

In *Arpactophilus*, the arrangement and shape of the spinnerets do not vary much among the species examined. They are branched, relatively short, and form a dense brush along the apex of tergum VI (Fig. 6). *Xysma* and some *Spilomena* have a condition similar to *Arpactophilus*, except that the spinnerets are less numerous, rel-

atively longer, and without branches. In most *Spilomena* and *Microstigmus*, however, the spinnerets also occupy part of the tergum disc, along its midline (Fig. 7). *Microstigmus* has simple, non-branched spinnerets that form a small tuft at the tip of the metasoma. In several groups of *Spilomena*, the spinnerets are arranged in two parallel or diverging rows over the tergum. Most commonly, these rows extend over the apical third of tergum VI, but in some species they almost reach the anterior border of the tergum (Fig. 8). In some cases, each spinneret can have several



Figs. 5-9. Silk glands and associated structures in members of the subtribe Spilomenina. 5. Class 3 glandular cells from *Microstigmus nigrophthalmus* (fixed material); scale = 50 μ m. 6. Posterior view of the metasoma of *Arpactophilus* sp., showing the brush of setiform spinnerets in the border of tergum VI (arrow); scale = 0.5 mm. 7. Dorsal view of tergum VI of *Spilomena* sp., showing the two rows of spinnerets along its midline (arrow); scale = 0.2 mm. 8. Lateral view of the metasoma of *Spilomena* sp., showing the spinnerets along the midline of tergum VI (arrow); scale = 0.5 mm. 9. Highly branched spinnerets in the border of the tergum VI of *Spilomena* sp. Scale = 20 μ m.

branches (Fig. 9). Another interesting modification found in some of *Spilomena*, as *S. formosana* Tsuneki, is the fusion of the spinnerets to form a pair of erect laminar structures, which are very thin, transparent, and fringed along their edge.

Most authors have erroneously interpreted the two rows of spinnerets on tergum VI of females of *Spilomena* as carinae

delimiting a pygidial plate. No species of *Spilomena* is known to have a pygidial plate, except *S. subterranea* and related undescribed species. When describing *S. subterranea*, McCorquodale and Naumann (1988) called attention to several features that this species does not share with other *Spilomena* or *Arpactophilus*. Dissection and clearing of tergum VI of a species closely

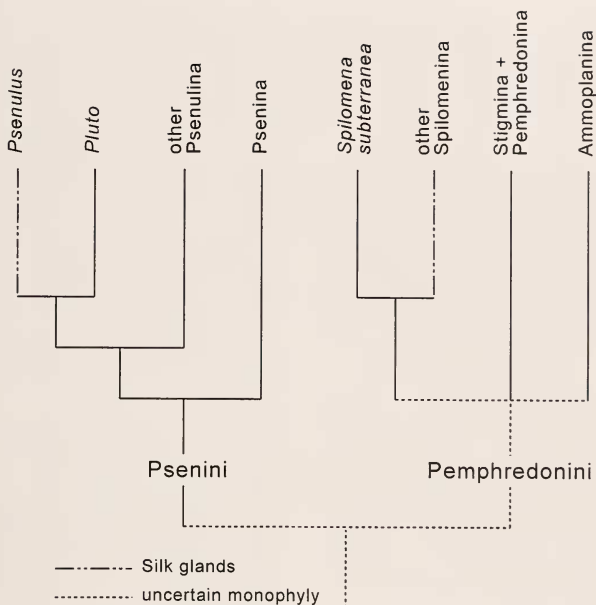


Fig. 10. Putative phylogeny for the major lineages of wasps of the subfamily Pemphredoninae [sensu Bohart and Menke (1976)]. Psenini based on Finnamore (1987); Pemphredonini based on Melo (in prep.).

related to *S. subterranea* revealed no evidence of silk glands. This could be considered a reversal (loss of the glands), but taking into consideration other features of *S. subterranea*, it seems more parsimonious to consider that this group of species diverged before the split that gave rise to the remaining *Spilomena* (including *Microstigma* and *Xysma*) and *Arpactophilus* (Melo, in prep.).

CONCLUSIONS

The silk glands in *Psenulus* and in the subtribe *Spilomenina* have many basic

features in common, like the morphology of the secretory cells (class 3 epidermal cells), the long excretory ducts, and the presence of spinnerets associated with the ducts. The position of the glands, however, differs: in *Psenulus*, the glands are associated with sternite IV and V, while in *Spilomenina*, they are associated with tergum VI (Fig. 4B). Also, branched spinnerets were observed only in members of *Spilomenina*. Despite the similarity in morphology, the silk glands in *Psenulus* and *Spilomenina* probably evolved independently (Fig. 10).

Future research in this group of wasps should investigate the ontogeny of the multicellular glandular unit and its associated spinneret, especially in species with multibranched and laminar spinnerets. Several studies on the development of epidermal glands composed of class 3 cells have revealed that each glandular unit is an isogenic group of cells derived, by successive mitosis, from one epidermal stem cell (Noirot and Quennedy 1991). It would be interesting to know whether the multicellular units found in pemphredonine wasps are formed by additional successive mitoses of a single stem cell, forming a large isogenic group, or by association of several isogenic groups derived from different stem cells.

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